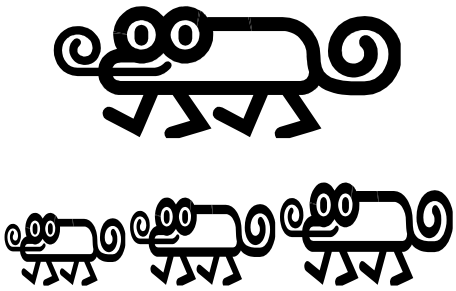
# An approach to understanding the role of maternal effects in adjusting to changes in environmental conditions

By

**Chloé D. Cadby-Bibari**



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**Statement of co-author contributions**

All Chapters and Appendixes of this thesis (except for the General Introduction and Discussion) have been prepared as scientific manuscripts for submission to peer-review journals as identified on the title page of each chapter. In all cases the design and implementation of the research, data analysis, interpretation of results and manuscript preparation was the responsibility of the candidate but was carried out in consultation with supervisors and other specialist contributors. These contributions are outlined for each chapter below.

**Chapter 2:** Cadby, CD is the principal author, carried out the analysis and contributed to data collection in the field and laboratory. While, GM helped with the analysis and writing and collecting data in the field. Hobday, AJ helped with the analysis and provided the SST and large indices values. Uller, T helped with concept and writing, and Wapstra, E helped with concept, writing and analysis and collected the majority of the data.

**Chapter 3, 4 and 5:** Cadby, CD conducted the field and laboratory data collection, analysis and is the principal author. Jones, SM and Wapstra, E both supervised Cadby, CD and helped with analysis, writing and data collection.

**Appendix 1:** Cadby, CD provided data for analysis and contributed to the writing. Uller, T is the principal author.

**Appendix 2:** Cadby, CD is the principal author with While, GM under the supervision of Wapstra, E. This work is based on Jungalwalla, T Honour's project and thesis which was done under the supervision of Wapstra, E and in collaboration with Peters, D.

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# Contents

**CHAPTER 1**

# General Introduction

The Intergovernmental Panel for Climate Change Fourth Assessment (IPCC 2007) reported an increase in mean global temperatures of about 0.7 °C in the last century and predicted an increase by 1.1 °C to 6.4 °C by the end of the 21st century. Increasing temperatures have induced changes in other climatic variables such as precipitation, wind patterns and extreme events (e.g. heat waves) (IPCC 2007) as well as changes in species interactions and community structures (reviewed in Hughes 2000). The extensive tradition of monitoring plants, birds and some insects, especially in the Northern Hemisphere, allowed the detection of significant responses to climate change (e.g. Menzel 2000, Lenoir *et al*. 2008). Significant trends and coherent (i.e. a globally coherent fingerprint) are emerging such as earlier breeding (Parmesan & Yohe 2003; Root *et al.* 2003; Moller *et al.* 2010) and species moving towards higher latitudes and altitudes (Parmesan *et al.* 1999, Hickling *et al*. 2006; Randin *et al.* 2009). In the long term, these changes are predicted to increase the vulnerability of species to extinction and to create major changes in ecosystem structure and function (Thomas *et al.* 2004, Thuillier *et al.* 2005, 2011; Van de Pol *et al.* 2010).

In Australia, we lack the long term monitoring that has allowed the detection of trends in species responses to climate change in the Northern Hemisphere (Hughes 2003). Because the impact of climate change depends on the environmental sensitivity of the organisms (Tewksbury *et al.* 2008; Deutsch *et al*. 2008; Huey *et al*.

2009; Beldade *et al*. 2011), the most efficient means of detecting climate-induced changes is by selecting indicator species that are highly sensitive to climate (Hughes 2003; Deutsch *et al*. 2008; Beldade *et al*. 2011). Reptiles are particularly indicated as model systems as they are ectotherms: most of their physiological processes are very sensitive to environmental conditions and underlie phenological responses and distribution patterns (Huey & Bennett 1987; Sinervo & Adolph 1989; Angilletta et al. 2002; Guisan & Hofer 2003; Arntzen 2006; Sinervo *et al.* 2010). For example, reproduction, foraging activity, basking behaviour, metabolism and growth rate are all processes that are very sensitive to climate and environmental factors and that are linked to fitness and survival (e.g. Huey & Bennett 1987; Burger & Zappalorti 1992; Litzgus *et al.* 1999; Angilletta *et al*. 2002; Kearney 2002; Bowen *et al.* 2005). Therefore, it is reasonable to predict that reptiles (and other climate sensitive species) will be affected by climate change and their persistence will depend on their ability to adjust or adapt to a new environment (Chevin *et al.* 2010; Sinervo *et al.* 2010; Beldade *et al.* 2011; Hofman & Sgro 2011; Hof *et al.* 2011).

Phenotypic plasticity, which can be defined as the phenomenon of a genotype producing different phenotypes in response to different environmental or developmental conditions, may be a key to species persistence as it can facilitate adjustment to new conditions and evolutionary adaptation (Przybylo *et al*. 2000; Ghalambor *et al.* 2007; Charmantier *et al*. 2008; Beldade *et al.* 2011). When a species is faced with new environmental conditions and its phenotypic response is a good match with the new environment, the species can adjust to the new conditions without a change in genotype (as there is no potential for selection to occur and therefore no evolution) (Ghalambor *et al.* 2007; Hofman & Sgro 2011; Hof *et al.*

2011). Alternatively, when the phenotypic plastic response produced is just below the optimum, it facilitates adaptive evolution by promoting population persistence until selection operates (Baldwin 1986; Pigliucci 2001; West-Eberhard 2003; Ghalambor *et al.* 2007; Hofman & Sgro 2011). In some cases, even when the plastic response is away from the optimum it can promote species persistence through selection for lack of plasticity and therefore through selection for lack of response to environmental factors (Ghalambor *et al.* 2007).

In reptiles, environmental factors (including climatic factors) are an important source of phenotypic plasticity and this is especially significant during embryonic development. For example, temperature, nutrition and stress during embryonic development affect a suite of phenotypic traits such as date of birth, sex, size at birth, mass at birth, limb length, anti-predatory behaviour, dispersal abilities and locomotor performance (e.g. Shine 2004, Massot *et al.* 2008, reviewed in Deeming 2004; Booth 2006) with potential long-term implications for individual fitness and consequences for population demographic effects (e.g. Warner & Shine 2007; Uller & Olsson 2010; Wapstra *et al.* 2010). Therefore, a change in climate and environmental factors (directly or indirectly linked to climate) will likely affect the embryonic development of reptiles and result in changes in phenotype. This phenotypic response resulting from climate change may benefit reptiles as illustrated in a recent long-term study: in the common lizard (*Lacerta vivipara*), the increase in temperatures of the past decades has resulted in females producing larger newborns, which has had a detectable positive impact on individual fitness and consequently population demography as larger newborn result in larger adults and larger adult females have greater reproductive output (Chamaille-Jammes *et al.* 2006).

Importantly, because environmental conditions have strong effect during embryogenesis, females (or in rare cases males) can influence what is experienced by the embryo and as a result the offspring phenotype. The interactions between a mother and her offspring that affect the offspring phenotype independently of the mother's genetic contribution are termed maternal effects. Maternal effects can include physiological (e.g. maternal hormones) or behavioural effects (e.g. maternal care) (Mousseau & Fox 1998; Marshall & Uller 2007; Uller 2008). Maternal influence over offspring phenotype makes reptiles particularly interesting to study in the context of climate change because maternal effects can play an important role in producing adaptive offspring phenotype in a new environment. For example, mothers can manipulate embryonic developmental conditions so that the offspring phenotype best fit the new environment (also known as maternal pre-programming) (Mousseau & Fox 1998; Marshall & Uller 2007; Uller 2008). Furthermore, maternal effects are themselves plastic responses to the environment. If they are adaptive, they can facilitate species adjustment to new environmental conditions. For example, maternal effects can buffer deleterious environmental conditions on embryonic development and therefore on offspring phenotype (Mousseau & Fox 1998; Marshall & Uller 2007; Uller 2008).

In oviparous species, field studies have already demonstrated that mothers can buffer changes in environmental conditions. For example, following a recent increase in soil temperature, female three lined skinks (*Bassiana duperreyi*) laid their eggs in deeper (i.e. cooler) nests allowing for partial compensation for the change in temperature (Telemeco *et al.* 2009). Viviparity in reptiles is thought to have evolved

as it allows increased and more refined control of embryonic developmental conditions (Shine 1983, 1995) as maternal influence can occur throughout gestation (i.e. it is not limited to egg-production and egg-laying). For example, mothers can control developmental temperatures by basking more or less depending on the external temperatures (Beuchat 1986; Robert & Thompson 2010) and can transfer metabolites, nutrients and hormones throughout gestation via the placenta (Swain & Jones 2000; Trexler & DeAngelis 2003; Thompson & Speake 2006; Itonaga *et al.* 2011a, 2011b). Therefore, viviparous females have arguably more opportunity than oviparous females to buffer embryonic development from deleterious environmental conditions and/ or to adaptively manipulate offspring phenotype. This is well illustrated in the viviparous lizard, *Lacetra vivipara*. If faced with predators during gestation, maternal transfer of stress hormones acts as a bridge between the maternal and the embryonic environment to pre-program offspring phenotype to live in stressful conditions. As a result offspring are born with increased risk-averse behaviour (Uller & Olsson 2006), which is beneficial in an environment with high predatory risks. This is less likely to occur in oviparous species where mothers can only sample the environment and deposit hormones in the yolk prior to egg laying.

Although maternal effects may play an important role in adjusting to climate change, they are plastic responses to environmental conditions. As a result, they are highly flexible and dynamic and can be both adaptive and non-adaptive (Mousseau & Fox 1998; Marshall & Uller 2007; Uller 2008). The adaptive nature of maternal effects will depend on the costs to mothers and the benefits to offspring (Marshall & Uller 2007; Uller 2008). It is important to note, that with viviparity and increased potential for maternal control, there is also increased potential for parent-offspring conflict as

the offspring genome is expressed during the maternal investment phase. A maternal effect can be regarded as a 'shared phenotype' that affects both maternal and offspring fitness simultaneously (Marshall & Uller 2007). Importantly, whilst maternal effects affect the fitness of both, it is predicted that selection will typically maximise maternal, rather than offspring fitness, particularly in species with no post-natal maternal care where the evolution of offspring counter-strategies may be less likely to evolve (Bernardo 1996, Marshall & Uller 2007). For example, we would expect the extent to which viviparous species will be able to compensate for increasing temperatures to depend on the costs associated with maternal thermoregulation such as increased predatory vulnerability (Wasptra & O'Reilly 2001) or decreased feeding and breeding opportunity (Kearney *et al.* 2009, Sinervo *et al.* 2010). Maternal hormones may also be passively transmitted as a side effect of the environmental conditions experienced by mothers rather than an adaptive response to the environment and can affect embryonic development (Marshall & Uller 2007; Uller 2008). Therefore in order to understand the role of mothers in adjusting to a new climatic envelope we need to understand the costs and benefits associated with producing adaptive phenotypic responses.

Widespread species are of particular interest when trying to understand the costs and benefits associated with producing adaptive phenotypic responses as well as when trying to understand the role of mothers in adjusting and adapting to new environmental conditions. In widespread species, populations living under different environmental conditions face different costs and benefits of producing adaptive phenotypes (Price *et al*. 2003; Ghalambor *et al.* 2007). For example, in water dragons (*Physignathus lesueurii*) females from warm regions lay their eggs in deep

nests (that are cooler) while females from cold regions lay their eggs in shallow nests (that are warmer) (Doody *et al.* 2006; 2009). The benefits of such behaviour are obvious: maternal nest choice buffers the temperature differences between cold and warm regions thus, allowing the species to become widespread (Doody *et al.* 2009). However, the costs of producing adaptive responses vary between regions. For example, laying eggs close to the surface is costly in term of predatory exposure while laying eggs in shallow nests is costly in terms of maternal energy expenditure (e.g. Burger & Zappalorti 1992).

Species that have become widespread have been able to successfully adjust to different environmental conditions. As a consequence, local adaptations are common in widespread species of reptiles (e.g. Bronikowski 2000, Uller & Olsson 2003, Caley & Schwartzkopf 2004). For example, juvenile garter snakes (*Thamnophis elegans*) grow faster in climatic conditions characteristic of their natal population (Bronikowski 2000) and water skink offspring (*Eulamprus quoyii*) grow faster if they experience the thermal conditions of their native population during embryonic development (Caley & Schwartzkopf 2004). Therefore, by studying widespread species, the evolutionary potential of populations can be assessed by spatial studies across climatic gradients involving transplants or common garden experiments (Ghalambor *et al.* 2007; Hofman & Sgro 2011). Although this does not indicate the speed at which adaptation can occur, it indicates the relative importance of plastic and genetic contributions to variation along a gradient (Hofman & Sgro 2011; Hof *et al.* 2011), which is crucial to understand population resilience to environmental changes (including climate change).

In this study, I use a widespread reptile, the spotted skink (*Niveoscincus ocellatus*), to understand the effects of environmental factors on phenotypic plasticity and the role of mothers in modifying these effects. I aim to understand the potential of species to adapt or adjust to new climatic conditions. *Niveoscincus ocellatus* is endemic to Tasmania, living in rocky habitat including man-made rock walls. It is a medium sized viviparous lizard (snout vent length up to 85mm), which mates in autumn and spring and females give birth to up to six young in summer (Wapstra *et al.* 1999; Wapstra & Swain 2001). Viviparity is thought to be advantageous in colder climates as it allows the maintenance of embryos at higher temperature than a nest (i.e. soil temperatures) (Shine 1983; Beuchat 1986; Robert & Thompson 2010). Importantly for the purpose of my work, viviparity allows further control than oviparity on the embryonic environment and, hence, should increase the potential for maternal manipulation of offspring phenotype (Shine 1995). Furthermore, *N. ocellatus* has significant placentotrophy, meaning it has significant transfer of nutrients, hormones and metabolites through the placenta (Thompson *et al*. 2001; Stewart & Thompson 2009) which again may allow increased opportunities for maternal manipulation.

In order to better understand what dictates the adaptive (or non-adaptive) response of mothers to environmental conditions, I study two populations located at the extreme of the species distribution: a coastal population that experience long summers and mild temperatures throughout the year and a highland population that experience short summers, long winters and cooler conditions. Past studies on the same populations have clearly demonstrated significant variation in life-history and reproductive traits between populations, reflecting a combination of phenotypic and

genotypic responses to environmental variation (Wapstra *et al*. 1999, 2009, 2010; Melville & Swain 2000; Wapstra & Swain 2001). For example, females from the highland population are typically larger, take longer to reach maturity, and give birth two to four weeks later than those from the coastal population (Wapstra *et al.* 2001). Furthermore, it was recently demonstrated that populations differ in sex determination mechanisms with the highland population exhibiting genetic-dependent sex determination and the coastal population exhibiting temperature-dependent sex determination due to differences in selection pressure resulting from climatic differences (Wapstra *et al.* 2009; Pen *et al.* 2010). Previous work has also demonstrated the sensitivity of embryonic developmental processes to environmental conditions. In particular, basking opportunity affects offspring phenotypic traits (Wapstra 2000; Wapstra *et al.* 2004, 2009) with potential long-term consequence on fitness and survival (Pen *et al.* 2010; Wapstra *et al.* 2010). My work will build on past field and laboratory studies to further our understanding of the effects of environmental factors during embryogenesis and the role of mothers in mitigating changes in environmental conditions.

## Thesis presentation

I have a total of four data/empirical chapters, a general introduction and discussion and two appendices. Studies are presented as chapters when I am the first author and principal investigator and are presented as appendices when I am not. The thesis is presented as follows:

Chapter Two examines the effects of climate on offspring phenotype of two climatically distinct populations of spotted skinks using the data from a ten year field study. Climate change is predicted to affect local and global weather patterns and

recent studies in mammals and birds show that some species can be more sensitive to global climate indices than to local weather. Therefore, I examine the effects of climate at a local, a regional (using Sea Surface Temperatures) and a global scale (using the Indian Ocean Dipole, Southern Oscillation Index) on offspring size at birth and date of birth. I show that *N. ocellatus* is more sensitive to local weather than global weather patterns and that date of birth is more sensitive to climate than size at birth.

My work then focuses on the effects of environmental factors likely to be affected by climate change. The following studies aim to further our understanding of the role of maternal effects in modifying the impact of climatic and environmental effects on offspring phenotype. To do so I use a set of three laboratory experiments.

Climate change will lead to changes in temperature, cloud cover and wind patterns (IPCC 2007) and as a consequence will result in changes in basking opportunity for reptiles. For example during field work, we noticed that very few reptiles were basking on cloudy, windy or cold days. Chapter Three therefore, focuses on the effects of basking opportunity on offspring phenotype of spotted skinks from two climatically distinct populations and on the role of mothers in manipulating offspring phenotype. The results show that maternal effects, in this case mediated via maternal basking behaviour, have evolved to buffer potentially deleterious variations in thermal conditions. Furthermore, the compensatory basking behaviour observed here may have allowed the widespread distribution of the species. Differences in maternal basking behaviour between populations may allow buffering differences in thermal conditions between populations: females from the mountain population are more

opportunistic in their basking behaviour than females from the coastal population thus compensating for the reduced basking opportunity of the highland. Nonetheless, local adaptation in maternal basking behaviour does not preclude the evolution of locally adapted thermal effects: offspring grow faster if they experienced the thermal conditions they would typically experience in their native environment.

Chapter Four looks at the effects of maternal diet quality on offspring phenotype of spotted skinks. The spotted skink is an opportunistic feeder but depends on swarms of insects especially during the breeding season (Wapstra & Swain 1996). Climate change, with changes in temperature and precipitation patterns will certainly lead to changes in the timing of those swarms and therefore in the quantity and quality of food (as described in other species (Visser *et al.* 2004; Visser & Both 2005)). This study demonstrates the ability of mothers to compensate for the potentially deleterious effects of a poor quality diet on offspring phenotype. Furthermore, I show that maternal diet during gestation allows pre-programming offspring phenotype to best fit the nutritional environment. Offspring that are placed in the same nutritional environment as their mother run and grow faster than offspring placed in a different nutritional environment than their mother. This is the first study to show maternal pre-programming to the nutritional environment in reptiles and indicates some potential for coping when faced with changes in diet quality.

Chapter Five examines the effects of chronic stress on offspring phenotype in the spotted skink using the stress hormone corticosterone. Recent studies in reptiles have suggested that climate change may lead to periods of stress (e.g. Sinervo *et al.* 2010). Typically, when climate change results in temperatures that exceed the lizards' preferred body temperature, lizards are forced to retreat in burrows, which

eventually becomes very costly (and stressful) especially during the reproductive season as it prevents them from foraging and accumulating enough resources for reproduction (Sinervo *et al.* 2010, see also Kearney *et al.* 2009 for similar logic). The adrenal hormone corticosterone typically has a positive influence on metabolism in stressful conditions by increasing stamina and mobilizing energy stores. However, chronic exposure to corticosterone during embryonic development is generally deleterious as it can decrease growth rate, immune function and cognitive abilities and increase anxiety and psychopathology. Nonetheless, maternal stress hormones during embryogenesis could act as a bridge between the maternal and the offspring environment allowing for maternal pre-programming of offspring phenotype to stressful conditions (as observed in Chapter Four). However, in this study mothers are not able to adaptively manipulate offspring phenotype in response to stress. Instead chronic stress reduced both maternal and offspring body condition, which could have potential negative follow on effects on fitness and survival.

Appendix 1 examines the differences in costs and benefits associated with maternal optimization of offspring quality between two populations that have evolved in climatically distinct regions. Using a combination of field and laboratory data, this study demonstrates how differences in selection pressure between populations and as a result of climate has impacted on the evolution of maternal effects.

Appendix 2 is a modelling study, which describes how climate change will affect reptiles' distribution. Using unique downscaled climatic projections (at a scale of 11km grid cells) we model the predicted distributions of six species of endemic snow skinks (*Niveoscincus* genus). The model suggests that the future change in climate will push all six *Niveoscincus* species towards higher altitudes, mostly

towards regions that were previously too cold for them, while forcing them to contract their range at lower altitudes. Overall this range shifts will lead to an overall decrease in the distribution by between 40% and 95% of Niveoscincus current range by 2050 and between 75% and 100% by 2080.

The General Discussion synthesises the main outcomes of my research (4 chapters and 2 appendices) by integrating the results from each study to provide an overview of how environmental effects can affect *N. ocellatus* and how maternal effects can promote species adjustment in changing environmental conditions.

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**CHAPTER 2**
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**CHAPTER 3**
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**CHAPTER 5**
**Are increased concentrations of maternal corticosterone adaptive to offspring? A test using a placentotrophic lizard**
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# CHAPTER 6

## General Discussion

There is clear evidence that climate change is affecting biological systems worldwide. Numerous studies report changes in species physiology, phenology and distribution as a result of climate change (reviewed in Hughes 2000; Walther *et al*. 2002; Root *et al*. 2003; Hitch & Leber 2006; Parmesan 2006). This thesis took an integrated approach to examining the effects of climate on the spotted snow skink (*Niveoscincus ocellatus*) in order to better understand how climate change might affect snow skinks (*Niveoscincus* genus) in particular and reptiles in general. Specifically, I investigated the role of maternal effects in modifying the impact of proximate environmental factors on embryonic development and the role of phenotypic plasticity in promoting species adjustment to new environments. Here, I take the opportunity to synthesise the main outcomes of my research by integrating the results from each study into an overall picture of how environmental heterogeneity affects evolutionary and ecological processes in reptiles.

In this study, I combined laboratory and long-term field observations to examine trends in the responses of *N. ocellatus* to environmental variation during embryonic development. I show that environmental factors including climatic factors have significant effects on date of birth, size at birth, locomotor performance and growth rate of the offspring (Chapters 2, 3, 4 & 5, Appendix 1). Those traits are typically related to fitness and survival in this species (Wapstra *et al.* 2010; Appendix 1) and in reptiles in general (Chamaillé-Jammes *et al*. 2006; Warner & Shine 2007; Uller &

Olsson 2010). Therefore, my results provide evidence that climate change is likely to have a significant impact on *N. ocellatus* and other reptiles.

In order to cope with climate change, species can either disperse to a suitable climatic envelope elsewhere (referred to as 'a "habitat tracking") (e.g. Parmesan & Yohe 2003; Hitch & Leberg 2006; Parmesan 2006; Beldade *et al*. 2011) or adjust to the new climatic conditions (Bradshaw & Holzapfel 2007; Kearney *et al*. 2009; Sinervo *et al*. 2010; Beldade *et al.* 2011; Hofman & Sgro 2011; Hof *et al.* 2011). Using a bioclimatic model, we predict that if *N. ocellatus* was to track its climatic envelope, under A2 climate change scenario, it would move towards higher altitudes mostly towards regions that were previously too cold, while simultaneously contracting its range at lower altitudes (Appendix 2). Overall, we predict that *N. ocellatus* range shifts will result in an average decrease of 40% of its current range by 2050 and of 60% 2080 (Appendix 2). Our model predictions are in accordance with predictions for other taxa, which suggest that species are moving towards higher altitudes and latitudes (Parmesan *et al.* 1999; Hughes 2000; McCarty 2001; Parmesan & Yohe 2003; Parmesan 2006; Thomas *et al.* 2006) and for reptiles, which suggest they are under considerable threat from changing environmental conditions (Pounds *et al.* 1999; Araújo *et al*. 2006; Hickling *et al.* 2006; Raxworthy *et al.* 2008; Huey *et al.* 2009; Sinervo *et al*. 2010, Foufopoulos *et al.* 2011). However, our model like most bioclimatic models assumes that the species is able to disperse and that its bioclimatic envelope is fully captured by its current distribution. This may not reflect reality as *N. ocellatus* may be unable to disperse (as suggested in other reptilian species, Araujo & Pearson 2005; Araujo *et al.* 2006) and/ or may be able to live outside its current range either because its distribution is currently limited by factors

other than climate such as geological or biological barriers (e.g. sea, inter-specific competition; e.g. Olsson & Shine 1998) and /or because it can adjust to a new climatic envelope (Kearney *et al*. 2009; Sinervo *et al*. 2010; Beldade *et al.* 2011; Hofman & Sgro 2011). If *N. ocellatus* is able to adjust to a new climatic envelope it may, in contrast to our predictions, expand its range in response to climate change by remaining in areas it currently occupies while colonizing new climatic regions.

Adaptive phenotypic plasticity is the key to adjusting to a new climatic envelope. Adaptive phenotypic plasticity can allow adjustment without a change in genotype (e.g. Przybylo et al. 2000; Ghalambor *et al.* 2007; Charmantier et al. 2008; Beldade *et al.* 2011; Hof *et al.* 2011) and can facilitate evolutionary adaptation through natural selection (e.g. Rodríguez-Trelles & Rodríguez 1998; Ghalambor *et al.* 2007; Beldade *et al.* 2011; Hofman & Sgro 2011). In reptiles, the environment experienced during embryonic development is the greatest source of phenotypic plasticity as it affects offspring morphological and behavioural traits (reviewed in Deeming 2004; Booth 2006; see Chapter 2, 3, 4, 5; Appendix 1). Importantly, mothers play a significant role in mediating the developmental environment (e.g. Shine 1995; 2004; Resetaritis 1996; Telemeco *et al*. 2009) and can thus contribute to adaptive phenotypic plasticity and promote population persistence in the face of climate change. In this thesis I investigated the potential for maternal effects to produce an adaptive phenotype.

*N. ocellatus* displayed two types of adaptive maternal effects: maternal pre-programming when *N. ocellatus* maternal nutritional environment produced offspring phenotype that matched the offspring nutritional environment (Chapter 4)

and maternal buffering of sub-optimal environmental conditions for embryonic developmental processes when gravid females actively changed their basking behaviour (Chapter 3) and used their own energy stores (Chapter 4) to compensate for the detrimental effects of reduced basking opportunity (Chapter 3) or poor quality diet (Chapter 4) on offspring size, body condition, growth rate and locomotor performance. Both types of maternal effects are considered to be adaptive as they result in increased offspring fitness (Mousseau & Fox 1998; Marshall & Uller 2007; Uller 2008) either through increased performance (i.e. pre-programming, Chapter 4) or stabilisation (i.e. maternal buffering, Chapter 3, 4) of fitness related traits such as growth rate and size at birth (Appendix 1; Chamaillé-Jammes *et al.* 2006). Similar results were reported in the oviparous three-lined skinks (*Bassiana duperreyi*) in which females laid their eggs earlier (when temperatures are cooler) and chose cooler, deeper nests in response to a recent increase in temperature (Telemeco *et al.* 2009). If mothers can produce adaptive response to changing conditions they may play an important role in species persistence in the face of climate change by reducing the costs of directional selection (e.g. Haldane 1957; Ghalambor *et al.* 2007; Telemeco *et al.* 2009; Kearney *et al.* 2009).

By reducing the costs of directional selection, adaptive maternal effects can facilitate the potential for evolutionary adaptation and colonization of new environment (including new climatic envelope) as they allows enough time for a population to become established for standing genetic variation in combination with mutation and /or recombination to provide a range of heritable phenotypes to respond to local selection pressures (Baldwin 1986; Pigliucci 2001; West-Eberhard 2003; Ghalambor *et al.* 2007; Hofman & Sgro 2011; Hof *et al.* 2011). As a consequence, local

adaptations resulting from adaptive phenotypic plasticity are commonly described in widespread species (reviewed in Price *et al*. 2003). In *N. ocellatus,* adaptive maternal behavioural and physiological plasticity (i.e. maternal buffering of unfavorable thermal and nutritional conditions) appear to have favored the widespread distribution of the species by serving as a bridge for the evolution of locally adapted maternal effects. I found that gravid females from the mountain population are more opportunistic in their basking behaviour and appear to have stronger canalisation of nutrient transfer than gravid females from the warmer coastal population (Chapter 3, 4 & Appendix 1).

In the mountains, where temperatures remain generally low, larger born offspring have a greater chance of survival than smaller offspring as this increases their chance of reaching winter in good body condition (as demonstrated in Appendix 1). Therefore, mountain mothers that respond appropriately to low temperatures by basking more and by increasing transfer of nutrients to the embryo are selected for because they produce large offspring. In contrast, mothers from coastal regions experience longer summers and milder temperatures throughout the year which relax selection pressure on size at birth of offspring and thus, on maternal compensation mechanisms (Appendix 1). Overall, population-specific maternal compensation mechanisms allow reducing the difference in climate between climatically distinct populations. Similarly, female water dragons (*Physignathus lesueurii*) lay eggs in deep (i.e. cool) nests at low altitudes (where it is warm) but in shallow (i.e. warm) nests at high altitudes (where it is cooler) thus, buffering the temperature difference between lower and higher altitudes populations (Doody *et al.* 2006; Doody 2009).

Not all maternal effects, however, result in adaptive phenotypic plasticity. The adaptive nature of maternal effects reflect the evolutionary outcome of the parent-offspring conflict (i.e. who wins, and at what cost?) (Mouseau & Fox 1998; Marshall & Uller 2007; Uller 2008; Badyev & Uller 2009). When the costs to mothers of increasing offspring fitness outweigh the benefits for the offspring, maternal effects generally result in non-adaptive phenotypic plasticity or passive transfer of the maternal environment (Mousseau & Fox 1998, Marshall & Uller 2007; Uller 2008; Badyev & Uller 2009). Importantly, the costs of increasing offspring fitness can vary between contexts and even between offspring traits such that some traits show adaptive plasticity while others do not (Marshall & Uller 2007; Ghalambor *et al.* 2007; Marshall 2008; Uller 2008). For example, in our system although maternal behavioural shifts appeared to compensate for the effects of basking conditions on size at birth (Chapter 3), date of birth was strongly affected by thermal conditions during gestation. Reduced basking opportunity resulted in later date of birth under both laboratory (Chapter 3) and wild conditions (Chapter 2).

The balance between the costs associated with increased basking behaviour such as increased predator vulnerability (especially for gravid females, see Wapstra & O'Reilly 2001) or decreased foraging opportunities (Huey & Slatkin 1976; Shine 1980; Downes 2001; Wapstra *et al*. 2009; Sinervo *et al*. 2010), and the benefits of reducing gestation length appear to have selected against further maternal buffering of thermal effects on embryonic developmental rate (see also Wapstra *et al.* 2010). The benefits of reducing gestation length may not be as great as that of producing large offspring. In Appendix 1, we show that heavier offspring had greater chances of survival from birth through hibernation and until the beginning of the following

spring (in the mountain populations at least). In contrast, there was no link between survival and date of birth (except in years when conditions were extreme, as described in a parallel study, Wapstra *et al.* 2010). Therefore, the weak selection on offspring date of birth may have maintained strong effects of maternal thermal opportunity on this trait resulting in passive temperature-induced phenotypic variation rather than adaptive phenotypic plasticity.

Even traits that are subject to consistent and strong selection may exhibit non-adaptive plasticity in contexts where environmental conditions are unpredictable, extreme or fall outside the range historically experienced (Marshall & Uller 2007; Ghalambor *et al.* 2007; Marshall 2008; Uller 2008). For example, unpredictable environments may select against maternal pre-programming because they significantly increase both the risks and the costs associated with transmitting the wrong information to the embryo and pre-programming offspring phenotype to the wrong environment (DeWitt *et al.* 1998; Marshall & Uller 2007; Ghalambor *et al.* 2007; Marshall 2008; Uller 2008). Unpredictable environmental conditions may have prevented females *N. ocellatus* from pre-programming their offspring to environmental factors such as basking opportunity (Chapter 3) and chronic stress (Chapter 5). I found no correlation between the thermal conditions (in this case maximum temperatures used as a surrogate for basking opportunities) experienced by female *N. ocellatus* during gestation and the thermal conditions experienced by their offspring during the first three months of life, at both sites used in the study (Chapter 3) (results of the correlation: coastal site, $r^2 = 0.12$, $P > 0.1$; mountain site, $r^2 = 0.06$, $P > 0.1$). This suggests that the thermal conditions experienced by gravid females during gestation do not predict the thermal conditions experienced by

offspring. Similarly, I found no evidence of maternal pre-programming to chronically elevated plasma corticosterone concentrations. One explanation may be that there is no selection for pre-programming to chronic stress in this species because the environmental conditions that induce chronic stress response in *N.ocellatus* adults may not induce stress in juveniles (e.g. adult-specific competition for territory or food or sexual harassment Le Galliard *et al*. 2005). In other words, there may be no advantage for mothers in pre-programming their offspring to stressful conditions they will not experience.

The costs of producing an adaptive phenotype may also increase when environmental conditions fall outside what individuals typically experience as individuals are not "wired" to compensate for those extreme conditions (DeWitt *et al.* 1998; Marshall & Uller 2007; Ghalambor *et al.* 2007; Marshall 2008; Uller 2008). In *N. ocellatus*, mothers were unable to compensate fully for thermal conditions that fell outside those experienced in their native range. Offspring growth rate was significantly reduced in individuals that experienced thermal conditions outside the species' historical range during embryonic development (Chapter 3). As a result, offspring from mountain populations grew faster if their mothers experienced cold temperatures during embryogenesis while offspring from coastal populations grew faster if they experienced mild temperatures during gestation, irrespective of the conditions they experienced postpartum (Chapter 3). Similarly, offspring from populations of eastern water skinks (*Eulamprus quoyii*), located at both the extremes of the species' distribution grew faster if their mothers have access during gestation to the basking opportunity they typically experience in their population of origin (Caley & Schwarzkopf 2004).

Importantly, climate change is predicted to result in extreme events that will increase climate variability (IPCC 2007). Species will increasingly be faced with environmental conditions that are unpredictable or fall outside their historical range, resulting in higher costs and risks associated with maternal buffering or maternal pre-programming. This is especially true for tropical reptiles whose range of thermal preferences has been canalized by previous selective regimes (Deutsch *et al*. 2008; Tewksbury *et al*. 2008; Huey *et al.* 2009; Sunday *et al.* 2011). Theoretical models (Kearney *et al.* 2009; Sinervo *et al*. 2010) predict that future increases in temperature will force tropical species to reside in constant shade if they are to remain within optimum temperatures. Residing in constant shade will increase the costs of thermoregulation (and compensation) by limiting breeding and foraging activity so strongly that it has been predicted it will lead those species to extinction (Pounds *et al.* 1999; Williams *et al.* 2003; Raxworthy *et al.* 2008; Kearney *et al.* 2009, Huey *et al*. 2009; Sinervo *et al.* 2010). Although the costs of thermoregulation may not be as high for temperate reptile species such as *N. ocellatus*, whose thermal range is considerably wider than tropical species (Addo-Bediako *et al.* 2000; Tewksbury *et al.* 2008; Sunday *et al.* 2011), my study demonstrates that unpredictable or extreme conditions do limit the ability of such species to respond adaptively.

Non-adaptive phenotypic plasticity can also lead to evolution and promote species' adaptation to new climatic conditions (Ghalambor *et al.* 2007; Badyev & Uller 2009; Pfennig *et al.* 2010; Salamin *et al.* 2010; Beldade *et al.* 2011; Hofman & Sgro 2011). When the optimum phenotype is never produced, selection favours canalized responses that allow organisms to produce the same phenotype regardless of

environment (i.e. lack of plasticity; Ghalambor *et al.* 2007). This is illustrated well in the sex determination mechanisms of *N. ocellatus* (Pen *et al*. 2010). In the coastal populations, temperature sex determination (TSD) (i.e. phenotypic plasticity of sex) has been selected for because temperature variation between years is low preventing the production of extremely biased sex ratio and because the fitness consequences of date of birth, which is determined by temperature, are sex-dependent: earlier birth benefits females but not males. Early born offspring are typically larger at maturity and larger females have higher reproductive output (Pen *et al.* 2010; see Chamaillé-Jammes *et al.* 2006) but larger males do not sire more offspring (Pen *et al.* 2010). In contrast, genotypic sex determination (GSD) which generates sex ratios that do not deviate from 1:1 is selected for in the highland populations because high fluctuation in climate between years would lead to significant bias in sex ratio and because fitness returns are not dependent on date of birth in either sex (Pen *et al*. 2010). Although I did not observe such clear-cut evidence of canalized responses in my study, I did observe differences in the effects of maternal thermal opportunity and maternal diet on offspring development between populations, which suggested selection for canalized responses in the mountain populations (Chapter 3, 4 and Appendix 1). For example, there was no effect of basking opportunity on offspring mass in the mountain population whereas poor basking opportunity consistently reduced offspring mass in the coastal population (Appendix 1). Those results may stem from the fact that mothers from the mountain population are more opportunistic in their basking behaviour and have canalized transfer of nutrients (as described earlier). However the results also suggest selection for canalization of phenotypic responses allowing the production of good quality offspring even when environmental conditions are poor during gestation (Chapter 3, 4, Appendix 1).

In conclusion, my study demonstrates the complexity and the flexibility of maternal effects. It also shows how maternal effects can promote species persistence in new environments. In *N. ocellatu,s* maternal effects differed in whether they produced adaptive or non-adaptive plasticity, depending on the trade-offs between the fitness costs to mothers and benefits to offspring which did vary between traits and contexts. Nonetheless, the population-specific adaptations observed in *N. ocellatus* and as a result its widespread distribution suggest this species has the potential to adjust to new climatic envelopes. Therefore, it is plausible that in contrary to our predictions (in Appendix 2) *N. ocellatus* will expand its distribution in response to climate change. It is important to note that phenotypic plasticity was often seen as being irrelevant or even a hindrance to adaptive evolution and even today relatively few studies have progressed from the view that plasticity is a nuisance parameter when measuring norms of reaction in the context of climate change (reviewed in Ghalambor *et al.* 2007; Chevin *et al.* 2010; Hof *et al.* 2011). Clearly, we must fully appreciate the potential role of phenotypic plasticity in promoting population persistence and incorporate phenotypic plasticity, including the costs and limits of that plasticity, in model of population persistence if we are to make reliable predictions as to the future of species in the face of climate change.

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# Appendices 1 and 2

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**APPENDIX 1**

**Altitudinal divergence in maternal thermoregulatory behaviour may be driven by differences in selection on offspring survival in a viviparous lizard**

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**APPENDIX 2**

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